Phytoplankton ecology of subarctic lakes in Finnish Lapland

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Academic dissertation

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Abstract

The climate is warming and it is most noticeable in the arctic and subarctic areas, where the warming trend is expected to be the greatest. Arctic and subarctic freshwater ecosystems, which are a very characteristic feature of the northern landscape, are especially sensitive to climate change. They could be used as early warning systems, but more information about the ecosystem functioning and responses are needed for proper interpretation of the observations. Phytoplankton species and assemblages could be especially suitable for climate-related studies, since they have short generation times and react rapidly to changes in the environment. In addition, phytoplankton provides a good tool for lake classifications, since different species have different requirements and tolerance ranges for various environmental factors. The use of biological indicators is particularly useful in arctic and subarctic areas, where many of the chemical factors commonly fall under the detection limit and therefore do not provide much information about the environment.

This work brings new information about species distribution and dynamics of subarctic freshwater phytoplankton in relation to environmental factors. The phytoplankton of lakes in Finnish Lapland and other European high-altitude or high-latitude areas were compared. Most lakes were oligotrophic and dominated by flagellated species belonging to chrysophytes, cryptophytes and dinoflagellates. In Finnish Lapland cryptophytes were of less importance, whereas desmids had high species richness in many of the lakes. On a Pan-European scale, geographical and catchment-related factors explained most of the differences in the species distributions between different districts, whereas lake water chemistry (especially conductivity, SiO_2 and pH) was most important regionally. Seasonal and interannual variation of phytoplankton was studied in the subarctic Lake Saanajärvi. Characteristic phytoplankton species in this oligotrophic, dimictic lake belonged mainly to chrysophytes and diatoms. The maximum phytoplankton biomass in Lake Saanajärvi occurs during the autumn, while spring biomass is very low. During years with heavy snow cover the lake suffers from a pH drop caused by melt waters, but the effects of this acid pulse are restricted to surface layers and last for a relatively short period. In addition to some chemical parameters (mainly Ca and nutrients), the length of the mixing cycle and physical factors such as the lake water temperature and the thermal stability of the water column had a major impact on phytoplankton dynamics. During a year with long and strong thermal stability, the phytoplankton community developed towards an equilibrium state, with heavy dominance of only a few taxa for a longer period of time. During a year with higher windiness and less thermal stability, the species composition was more diverse and species with different functional strategies were able to occur simultaneously.

The results of this work indicate that although arctic and subarctic lakes in general share many common features concerning their catchment and water chemistry, big differences in biological features can be found even in a relatively small area. It is most likely, that lakes with very different algal flora do not respond in a similar way to differences in the environmental factors, and more information about specific arctic and subarctic lake types is needed. The results also show considerable year to year differences in phytoplankton species distribution and dynamics, and these changes are most probably linked to climatic factors.

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List of original publications

This is a summary of the key findings of the original publications, which are referred to by their Roman numerals in the text.

I Tolotti, M., Forsström, L., Morabito, G., Thaler, B., Stoyneva, M., Cantonati, M., Sisko, M. & Lotter, A. (2006). Biogeographical characterisation of phytoplankton assemblages in high mountain and high latitude European lakes. *Archiv für Hydrobiologie* (Submitted manuscript).

II Forsström, L., Sorvari, S. & Korhola, A. (2006). Phytoplankton in subarctic lakes of Finnish Lapland – implications to ecological lake classification. *Archiv für Hydrobiologie* (in press).

III Forsström, L., Sorvari, S. & Korhola, A. (2005). The role of the environmental factors in controlling the Chrysophyte species distribution and biomass structure in subarctic lakes of Finnish Lapland. *Nova Hedwigia, Beihefte 128: 179-188.*

IV Forsström, L., Sorvari, S., Korhola, A. & Rautio, M. (2005). Seasonality of phytoplankton in subarctic Lake Saanajärvi in NW Finnish Lapland. Polar Biology 28: 846-861.

V Forsström, L., Sorvari, S., Rautio, M., Sonninen, E. & Korhola, A. (2006). Changes in physical and chemical limnology and plankton during the spring melt period in a subarctic lake. (Submitted manuscript)

Contributions

Major contributions of authors to the original papers. LF = Laura Forsström, MT = Monica Tolotti, MC = Marco Cantonati, BT = Berta Thaler, GM = Giuseppe Morabito, MSt = Maya Stoyenva, MSi = Miljan Sisko, AL = Andy Lotter, AK = Atte Korhola, SS = Sanna Sorvari, MR = Milla Rautio, ES = Eloni Sonninen.

Paper I
Original idea: MT, LF, MC, BT, GM, MSt, MSi AL
Study design & methods: MT, LF, MC, GM, MSi, BT, MSt, AL. Sampling design and strategies have been defined by the partner consortium of the EU Emerge Project.
Material collection: LF, MT, MSi, GM, BT, MSt, MC, AL
Analyses: MT, LF, MSi, BT, MSt, GM, MC, AL
Manuscript preparation: MT, LF, MC, GM, MSi, BT, MSt, AL.

Paper II
Original idea: AK, SS, MR, LF
Study design & methods: SS, MR, LF, AK
Material collection: LF, SS, MR, RLA
Analyses: LF
Manuscript preparation: LF, SS & AK commented on the text

Paper III
Original idea: AK, SS, MR, LF
Study design & methods: SS, MR, LF, AK
Material collection: LF, SS, MR, RLA
Analyses: LF
Manuscript preparation: LF, SS & AK commented on the text

Paper IV

Original idea: AK, SS, MR, LF
Study design & methods: LF, SS, MR
Material collection: LF, SS, MR
Analyses: LF
Manuscript preparation: LF, SS & AK, MR commented on the text

Paper V

Original idea: SS, MR
Study design & methods: SS, MR
Material collection: SS, MR
Analyses: LF, MR (zooplankton), ES (oxygen isotopes)
Manuscript preparation: LF, AK, SS, MR

1 Introduction

The importance of arctic and alpine lakes as the least impacted freshwater ecosystems was expressed already 50 years ago (Thomasson 1956). As most of the arctic and subarctic lakes are located in remote places, they generally do not suffer from severe direct human impact. Unfortunately many recent threats to the environment act on a global scale, and both the observed and projected increases in temperature are greatest in arctic areas (ACIA 2005, Smol et al. 2005). In the Arctic there are several feedback processes (ice- and snow-albedo, thawing of permafrost, cloud formation), which greatly affect and amplify the global climate change. In addition to changes in temperature, also precipitation is expected to increase and permafrost to thaw (ACIA 2005). These changes will result in a longer and warmer ice-free season as well as an increased nutrient and carbon input from the catchment areas. In response to the temperature increase, longer open water period and enhanced supply of nutrients, the total primary production is likely to increase in arctic and subarctic lakes and ponds (Hobbie et al. 1999, Flanagan et al. 2003).

Because of their small drainage areas, extreme climatic conditions and simple ecosystems, arctic and subarctic lakes are presumed to be especially sensitive to environmental changes (Douglas & Smol 1994, Rouse et al. 1997, Hobbie et al. 1999, Battarbee et al. 2002, Psenner et al. 2002, Smol et al. 2005). These ecosystems with low species numbers (especially in higher trophic levels) can be strongly affected if one of the few species has a strong response to the climate, whereas in a more complex ecosystem with a high number of species interactions it is more likely that there are some compensating species (Blenckner 2005). Since there are many arctic species that already live near their upper temperature limit and are especially well-adapted to prevailing environmental conditions, it is probable that some of them will die out or be replaced by competing southerly species (ACIA 2005).

Lakes and ponds are a major component of the northern landscape, but detailed studies concerning these ecosystems are rare, most comprehensive being the works done in tundra ponds and other freshwaters of Alaska (Hobbie 1980, Milner & Oswood 1997). Especially the interactions of climatic factors with arctic ecosystems are poorly understood, making it very difficult to project the possible effects of climatic change in these highly sensitive systems. Many biological processes are directly or indirectly temperature-dependent, e.g. phytoplankton growth rates are directly affected by variations in temperature and indirectly by changes in the underwater light climate induced by changes in thermal stratification (Reynolds 2006). The organisms at the lower end of the food web with short life-cycles are the ones which react most rapidly to any changes in their environment, making phytoplankton communities especially suitable for climate-related studies (Elliott et al. 2005).

Although the primary production and biomass of phytoplankton in high-latitude water bodies is usually low due to low temperatures, low nutrient availability and a short growing season, the phytoplankton communities form an integral part of the functioning of these sensitive ecosystems. Despite the harsh environments, phytoplankton communities can be very diverse representing various taxonomical groups and life-strategies (e.g. Holmgren 1983). Since different species have different preferences and tolerance ranges of various environmental factors, knowledge of the species composition of phytoplankton can be used in lake classifications and ecological status assessments (Willén et al. 1990). The aim of this thesis is to get more detailed information on the biogeography and dynamics of phytoplankton in northern lakes located above the treeline. This information is necessary as a basis for studies concerning climate change and other stressors and their effects on the biota.

1.1 Different definitions of the study area – arctic vs. subarctic

There are several criteria which could be used to delimit the arctic or subarctic areas, and many attempts have been made to come up with a comprehensive definition (Polunin 1951, Pechlaner 1971, Ahti 1980). The most appropriate definition depends much on the purpose, and the same area could be named differently based on the criteria used. Originally, the word "Arctic" comes from the Greek word *arktos* (bear, *Ursus*), after the constellations of Ursa major and Ursa minor, which are visible year round in the northern sky. The Arctic is often defined by the Arctic or Polar Circle (66˚32'N), which is the latitude at which the sun does not set on the summer solstice. However, this definition is too simplifying for ecological purposes, given the large variations in (among others) temperature, precipitation and topography that occur in this area. Climatologically the Arctic can be defined as the area north of the 10˚C July isotherm, which diverges from the Arctic Circle mostly due to ocean currents: for example Finland extends north of the Arctic Circle but lies south of the 10˚C July isotherm (Figure 1). The most common vegetational boundary for the Arctic region is the treeline, meaning the transition zone between continuous boreal forest and open tundra. This transition zone is very narrow in certain parts of North America, but can be up to 300 km wide in northern Russia (Stonehouse 1989). In addition, the treeline is often determined by altitude rather than latitude, and arctic-like conditions are found on mountainous areas far south. South of the Arctic is the Subarctic, which can be defined as the area between the closed-canopy boreal forest and the treeline. In general, the southern boundary of the subarctic corresponds with the southern limits of the discontinuous and sporadic permafrost.

Figure 1. The limits of the Arctic according to various definitions (AMAP 1998).

In addition to the terms arctic and subarctic, many others have been used for the same or comparable areas. For example Pechlaner (1971) includes lakes located in Alps, Pyrenees, Mt. Rainier (USA), Tatra and Lapland in his study of phytoplankton in high-mountain lakes. According to Pechlaner (1971) high-mountain area is synonymous to alpine horizon and means the zone above the timberline of mountains throughout the world. He defines polar lakes as lakes at sea level north or south of the timber line and arctic lakes as lakes beyond the Arctic

Circle. In the context of phytoplankton studies, high-altitude or high-latitude lakes have been described, among others, as arctic, subarctic, mountain, arctic-alpine, northern, high mountain, alpine, subalpine, polar and high-elevation lakes (e.g. Pechlaner 1971, Kalff et al. 1975, Moore 1979, Holmgren 1983, Eloranta 1986, Duthie & Hart 1987, Goldman et al. 1989, Nauwerck 1994, Salmaso & Decet 1997, Larson et al. 1998). In his study of climatic classification of Finland, Solantie (1990) divides northern Finland into northern boreal and hemiarctic zones, the latter covering only the Kilpisjärvi region in Northwest Finland. The hemiarctic zone is characterised by the sum of effective temperature below 390 ˚Cd, summer floods and drifting of snow due to lack of trees (Solantie 1976, 1980, 1990).

In this study the Finnish Lapland is considered subarctic, although especially the lakes located near or above 1000 meters elevation are more of an arctic-alpine nature from the perspective of the climate and vegetation in the area. Based on the phytogeographical definition (Kalliola 1973) the area above the northern treeline is considered arctic only when the latitude solely determines the treeline position, while in Fennoscandia altitude is responsible for the formation of the treeline.

1.2 Arctic and subarctic lakes as phytoplankton habitats

The most prominent feature of the subarctic and arctic areas is the extreme seasonality. The long, dark and cold winter is followed by a short summer with continuous sunlight. In general, the amount of precipitation in the arctic and subarctic areas is low, typically 200–400 mm yr^{-1} and most of it comes in the form of snow. The winter accumulation of snow leads to a brief (2–3 weeks) but intensive run-off during the melting period in the spring, when large amounts of melt waters may cause a rapid decline in the surface lake water pH (Kinnunen 1990, Thorsten 1998, Sorvari et al. 2000). The interannual variation in climatic factors, such as temperature and precipitation can be substantial, which is seen e.g. in the long-term data series of snow thickness in the Kilpisjärvi region (Figure 2). The main reason behind the interannual variation in weather and climate around the Northern Hemisphere is the North Atlantic Oscillation and Arctic Oscillation (Hurrell & Van Loon 1997, Thompson et al. 2000).

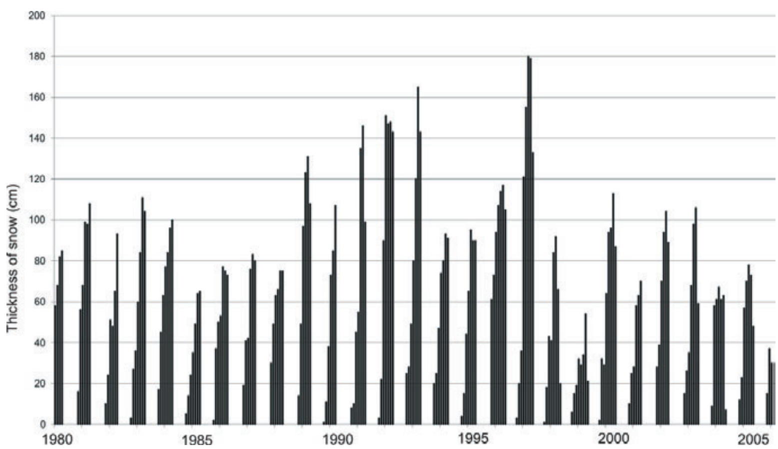

Figure 2. Monthly variation (October – April) of the snow cover thickness in Kilpisjärvi region between years 1980 and 2005. Data acquired from Finnish Meteorological Institute (1980-1995) and (1996-2006).

Most arctic and subarctic lakes are small and shallow, and have small and barren catchment areas (Moore 1978, Kling et al. 1992, Pienitz et al. 1997, Korhola et al. 2002, Rühland et al. 2003) (Figure 3). Low temperatures lead to extended periods of ice cover and, because of the ice and snow, reduced light penetration into the water during the spring. The length of the open water season varies from a few weeks to a few months, and in the High Arctic the lakes can be frozen all year round (Welch 1991). Low temperatures not only shorten the growing season, but also slow down many biological processes. Generally the lakes are dimictic or do not stratify because of their shallowness or coldness (Pechlaner 1971, Shortreed & Stockner 1986, Sorvari et al. 2000, Korhola et al. 2002, Rühland et al. 2003).

Arctic and subarctic lakes are typically oligotrophic or ultraoligtrophic clearwater lakes with low conductivity, alkalinity, nutrient and dissolved organic carbon (DOC) concentrations and circumneutral pH (e.g. Schindler et al. 1974, Shortreed & Stockner 1986, Forsius et al. 1990, O'Brien et al. 1997, Duff et al. 1999, Hamilton et al. 2001, Korhola et al. 2002, Lim & Douglas 2003). There are generally no dramatic variations in chemical properties during the short summer period (Nauwerck 1994, Sorvari et al. 2000) whereas the spring is a very dynamic season in many ways, e.g. by bringing the dilute meltwaters into the lakes (Catalan et al. 2002). Although lakes are oligotrophic, oxygen levels may be low during late winter/early spring as aeration is prevented due to thick ice and snow cover (Catalan et al. 2002). Low temperatures together with low nutrient availability and a short growing season mean that primary productivity is usually low and food webs consist of relatively small numbers of species arranged along few trophic levels (Welch 1991). Clear water, shallowness and oligotrophy of the water column create good conditions for periphytic communities and, in contrast to temperate lakes, periphyton can be responsible for a large proportion of primary production especially in arctic and subarctic ponds and shallow lakes (Figure 4)

Figure 3. Picture of a typical arctic lake in Finnish Lapland, Lake Vuobmegasvarri taken on 19th August 2004. The lake area is 1.2 ha. Photo: L. Forsström.

(Kalff & Welch 1974, Niemi 1996, Rautio & Vincent 2006). The short open water season, low nutrient levels and low water temperature restrict the occurrence of macrophytes, and their biomass and production is generally very low in subarctic lakes (Solander 1983). Zooplankton grazing may limit phytoplankton biomass and growth occasionally also in arctic lakes, especially in shallow lakes and ponds where the lack of predators and utilization of additional (benthic) food resources may lead to a high zooplankton biomass (Federle et al. 1979, Bertilsson et al. 2003, Flanagan et al. 2003, Rautio & Vincent 2006).

1.3 Phytoplankton in subarctic lakes

Phytoplankton communities in arctic and subarctic lakes are an outcome of low temperature, low conductivity, alkalinity and nutrient availability. Primary productivity is usually low, about 10–14 g C m^{-2} yr^{-1} (Duthie & Hart 1987, Miller et al. 1986). In concordance, the maximum phytoplankton biomass is low, < 1 mg l^{-1} wet weight (< 1000 mg m^{-3}) (Moore 1979, Eloranta 1986, Kalff et al. 1975). A characteristic feature for the transparent arctic and alpine lakes is the deep water maximum of chl-a and phytoplankton biomass (e.g. Pechlaner 1971, Tilzer 1972, Simona et al. 1999, Tolotti 2001, Catalan et al. 2002). The most likely cause for the higher algal densities found within or just under the thermocline are the higher nutrient concentrations and more stable environmental conditions (Hinder et al. 1999). Also, the light levels, including UV radiation, at the lake surface can be too high for an optimal photosynthesis rate (Milot-Roy & Vincent 1994, Callieri et al. 2001, Van Donk et al. 2001). The species number ranges from under 20 to more than 100 per lake (Table 1), and has been found to correlate with latitude, altitude or water temperature, while species composition is mainly determined by water chemistry (Moore 1979, Nauwerck 1994). Chrysophyta (golden-brown algae) is often the most dominant algal group, both in terms of cell densities and total biomass, but also diatoms, dinoflagellates and cryptophytes can be dominant or subdominant (Table 1) (Moore 1978, Eloranta 1986, 1995, Holmgren 1983).

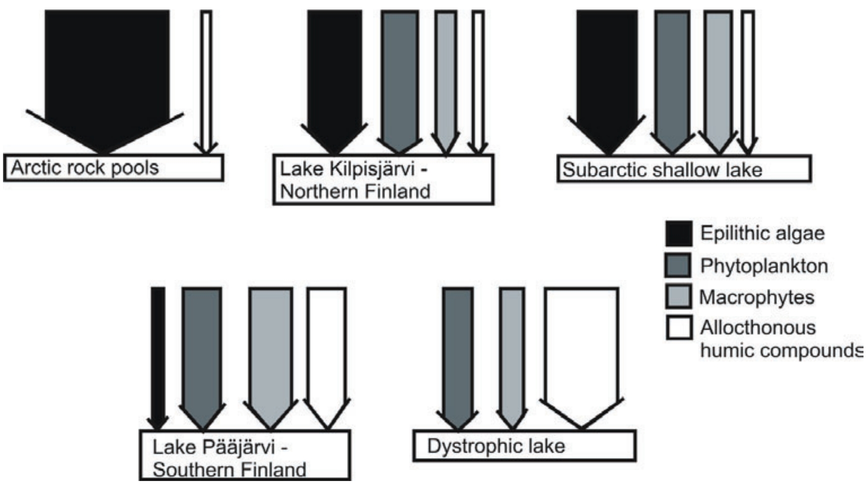

Figure 4. Schematic presentation of the relative importance of different primary producers and allochthonous humic compounds as contributors of biogenic energy in different types of lakes. Redrawn from Niemi 1996.

Table 1. Phytoplankton species numbers, maximum biomass and dominant algal groups in previous studies on arctic and subarctic lakes.

Location	Species number	Maximum biomass (mg m^{-3})	Dominant algal group	Reference
Toolik Lake, Alaska	136	n.d.	Chrysophyceae	O'Brien et al. 1997, Miller et al. 1986
Subarctic Canada	n.d.	70-340	Chrysophyceae – Bacillariophyceae	Duthie & Hart 1987
Subarctic Canada	19	300	Chlorophyta – Bacillariophyceae	Sheath et al. 1975
Arctic and subarctic Canada	60-75	75-190	Chrysophyceae – Bacillariophyceae	Moore 1979
Northern Sweden	18-47	n.d.	Chrysophyceae - Cryptophyceae	Nauwerck 1994
Northern Sweden	200*	400-900	Chrysophyceae – Bacillariophyceae/Dinophyceae/ Cryptophyceae	Holmgren 1983
Northern Finland	31-99	430-1000	Chrysophyceae	Eloranta 1995
Northern Finland	58	90-1100	Bacillariophyceae	Heinonen 1980
Iceland	n.d.	n.d.	Bacillariophycae – Chrysophyceae	Jónasson et al. 1992
Spitzbergen (Svalbard)	n.d.	n.d.	Chrysophyceae – Cryptophyceae	Laybourn-Parry & Marshall 2003
Faroe Islands	16-35	84-211	Cryptomonads, chrysomonads	Brettum 2002

* sum of three lakes

1.3.1 *Chrysophyta*

The phylum Chrysophyta (Chrysophyceae and Synurophyceae) consists mainly of unicellular or colonial flagellates that are restricted to freshwater planktic habitats (Sandgren 1988). They are very diverse both in their morphology (size, shape, colony-formation) and in their nutritional strategies (many species are able to switch between autotrophy and heterotrophy) (Holen & Boraas 1995). Chrysophytes are found in many kinds of water bodies, but they are especially characteristic of oligotrophic lakes with low summer water temperatures, low alkalinity and conductivity, and neutral or slightly acid pH (Sandgren 1988). When comparing the algal composition of different areas of Finland, Eloranta (1995) found that the relative proportion of chrysophyte biomass to the total phytoplankton biomass was highest (38%) in subarctic lakes of northern Lapland. Similar results have been found in the classification study of oligotrophic Swedish lakes (Willén et al. 1990). The biogeography of especially the silica-scaled chrysophytes has been studied intensively (e.g. Eloranta 1995, Kristiansen 2001), but still relatively little is known of the ecology and physical limitations of individual species, especially the non-scaled ones. Chrysophyceaen microfossils (siliceous scales and cysts) are well preserved in sediments and are used as paleolimnological indicators (Zeeb & Smol 2001), thus further increasing the need to understand the requirements of the vegetative cells that produce the cysts.

1.3.2 *Other main phytoplankton groups in the arctic*

Diatoms (Bacillariophyceae) can locally and temporally constitute an important part of arctic and subarctic phytoplankton. Along with chrysophytes, diatoms are good competitors for nutrients, especially phosphorus, but unlike chrysophytes they have obligate requirements for sufficient silica concentrations (Sommer 1983). Because of their silica frustules, diatoms are relatively heavy, and being mainly non-motile they rely on turbulence in order to remain in the photic layer (Sommer 1988). Dinoflagellates (Dinophyceae) have several characteristics which make them relatively competitive in low nutrient levels: the capacity of luxury consumption of phosphorus, the ability to search for nutrients from the whole water column by vertical migration, the diverse nutrient uptake strategies, and long generation times (Pollingher 1988). During unfavourable conditions, dinoflagellates are able to produce resting cysts. Contrary to chrysophytes, diatoms and dinoflagellates, cryptophytes (Cryptohyceae) have generally relatively high demands for nutrients (Sommer 1983), but a few species are common in arctic and subarctic oligotrophic lakes. Cryptophytes are sensitive to grazing, and the low grazing pressure of most arctic lakes is probably an advantage to these rapidly growing algae.

1.4 Subarctic lakes vs. alpine lakes as habitats for phytoplankton

Many studies have noted the similarity of alpine and arctic/subarctic lakes and their phytoplankton communities (Thomasson 1956, Nauwerck 1966, Pechlaner 1971), and similarities can be found even between phytoplankton communities of some arctic and acidic boreal lakes with clear water and low conductivity, both lake types being usually dominated by chrysophytes (Eloranta 1986). According to Nauwerck (1994) the Abisko region in northern Sweden (which is very similar to the Kilpisjärvi area) located at 1000 meters elevation roughly corresponds to 3000 meters elevation in the Alps in terms of climate and biological conditions. However, there is an important difference between these areas in terms of light. Arctic areas are subject to large seasonal variations in light availability, from total darkness in winter to continuous light in summer. In contrast, alpine lakes experience higher radiation levels with increasing altitude, but less seasonal variation in the day length. The ice cover period is shorter in alpine lakes, and they experience a longer stratification period with higher water temperatures during the summer (Table 2). Alpine lakes are also more often influenced by human activities, such as damming, pasture and tourism (Tolotti 2001, Catalan et al. 2002). They also receive larger amounts of air pollution (Curtis et al. 2005). As a consequence, alpine lakes show larger variation in productivity than arctic lakes.

The finding that even the remote arctic and alpine lakes are affected by anthropogenic impacts lead to EU funded projects AL:PE, AL:PE 2 and MOLAR, dealing with acidification,

Table 2. Characteristics of subarctic and alpine lakes.

	Subarctic lakes	Alpine lakes
trophic status	oligotrophic-ultraoligotrophic	oligotrophic-mesotrophic
lake morphology	small, shallow	small, shallow
pH	neutral/slightly alkaline	neutral/slightly alkaline
length of the open water season (months)	1-4	4-7
daylength during summer (h)	24	14-16
maximum algal biomass	< 1000 mg m^{-3}	usually < 1000 mg m^{-3}, but up to 6300 mg m^{-3} has been recorded
dominant algal group	mainly Chrysophyceae or other flagellates	mainly Chrysophyceae or other flagellates
time of maximum algal biomass	end of the ice free period/end of the ice cover period	end of the ice free period/ end of the ice cover period

climate and the response of high mountain lakes to environmental changes. In addition, an extensive survey of environmental and biotic features of a large number of lakes distributed in 15 European countries was made within one of the latest EU projects concerning high-mountain and high-latitude lakes (EMERGE). The author of this work has been involved in MOLAR and EMERGE projects.

1.5 Previous studies on subarctic phytoplankton

Phytoplankton flora of Finnish Lapland has been previously studied by Levander (1901, 1905), Järnefelt (1934, 1956), Luther (1937), Kristiansen (1964), Arvola (1980), Heinonen (1980), Tolonen (1980), Eloranta (1986, 1995) and Lepistö (1995). Especially the earliest studies are mostly descriptive and based on very few samples, and the studied lakes are mostly situated below the treeline and in Eastern Lapland. The phytoplankton of lakes in Swedish Lapland has been studied by Skuja (1964), Nauwerck (1966, 1968, 1980, 1994) and Holmgren (1983) and in North America by e.g. Alexander et al. (1980) and O'Brien et al. (1997). Most of the studies concerning arctic or subarctic phytoplankton have been conducted in Canada, where e.g. Moore (1978, 1979, 1980a, 1980b, 1981a, 1981b) has studied the role of environmental factors in the distribution and seasonality of phytoplankton, Kalff (1967a, b), Kalff & Welch (1974) and Kalff et al. (1975) the phytoplankton abundance and dynamics of natural and polluted ponds and lakes, and Sheath & Munawar (1974) and Sheath et al. (1975) the phytoplankton composition and periodicity in small subarctic lakes.

As in Finnish Lapland, also elsewhere the early studies focused on reporting the occurrences of various phytoplankton species, and were often based on single or very few net-samples with no or a very limited set of limnological data. More comprehensive studies on the arctic phytoplankton ecology are still quite rare, and especially experimental studies on arctic and subarctic phytoplankton are few in number. Experimental studies have been conducted on the effects of UV radiation (Van Donk et al. 2001), acidification (Schindler et al. 1981) and eutrophication (Holmgren 1983). In order to really understand how these systems operate and how they respond to environmental factors, it is necessary to gather more detailed information on seasonal and interannual changes, to include more geographical, environmental and biological factors in the studies, to sample lakes from various locations in order to get a more representative picture of the species distribution, and to conduct carefully designed experimental studies as well as long-term monitoring.

1.6 Conceptual background of the thesis

1.6.1 Succession and seasonality

The term succession originates from terrestrial plant ecology, where a series of predictable stages from pioneer to climax association can be found. The succession can further be divided into autogenic succession, which occurs as a result of biological processes, and into allogenic succession, which occurs as a result of changing external conditions (Begon et al. 1996). If succession is defined as "the non-seasonal, directional and continuous pattern of colonization and extinction on a site by species populations" (Begon et al. 1996), it is not well applicable to phytoplankton seasonality.

According to Reynolds (2006), the term succession should be used only when dealing with autogenic processes. However, the terms succession and seasonal succession has been widely used in connection with phytoplankton seasonality (e.g. Sommer 1989). Other terms used in the literature dealing with seasonal changes in phytoplankton include periodicity (Reynolds 1980), dynamics (Laybourn-Parry & Marshall 2003), and fluctuations (Sheath et al. 1975). Despite the conflicting terminology, it has long been widely recognised that phytoplankton species follow a certain recurrent periodicity which is linked to seasonal changes in their living environment. Based on these recognisable patterns in plankton seasonality, a PEG (Plankton Ecology Group) -model was developed to describe the seasonal changes in phytoplankton and zooplankton in an idealized temperate lake (Sommer et al. 1986). In contrast to temperate lakes which usually have two annual phytoplankton peaks (spring and autumnal maxima), the limited growing season of arctic lakes often results in a single maximum of phytoplankton biomass, either during the spring, sometimes already under ice, or during the autumn mixing period (Pechlaner 1971, Kalff et al. 1975, Miller et al. 1986, Shortreed & Stockner 1986).

1.6.2 Functional groups

The classical concepts of community ecology used in terrestrial ecosystems, such as MacArthur & Wilson's (1967) r- and K-selection and Grime's (1979) life-history-strategies of plants (C S R), have been first applied to phytoplankton ecology by Margalef (1978), Kilham & Kilham (1980), Reynolds (1980, 1988) and Sommer (1981). Reynolds et al. (1983) introduced a third category (w) into r- and K-strategies, to describe the mixing-tolerant species. Later, Reynolds (1988) proposed that r-, K- and w- strategies correspond to Grime's (1979) C-, S- and R- strategies of evolutionary adaptation of plants. Basically, different phytoplankton species are either specialized to rapid growth and reproduction (C), tolerating low amounts of essential resources (nutrients) (S), or tolerating frequent or continuous turbulence (R). The three strategies can be seen as apices of a triangle, whose primary axes reflect resource availability and disturbance (Fig. 5). The basic characteristics of primary strategies of phytoplankton are listed in Table 3.

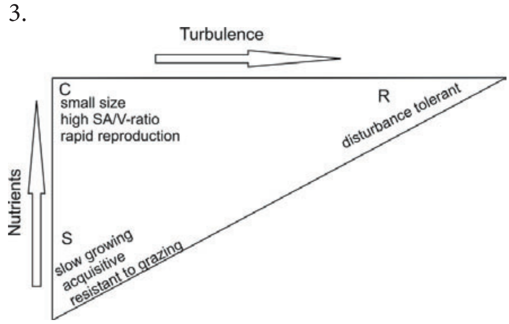

Figure 5. Graphical presentation of the CSR-functional theory (after Reynolds 1988).

In order to more precisely describe the periodicity of phytoplankton assemblages in different kinds of water bodies, Reynolds (1984a) described a number of species groups consisting of species that tend to have relatively similar seasonal sequences. This approach was further evolved into a comprehensive list of phytoplankton functional associations or functional groups (Reynolds et al. 2002, Reynolds 2006). Functional groups consist of species with similar morphology and environmental requirements, but they do not necessarily belong to the same phylogenetic group. In contrast to long species lists or usage of dominant taxonomical groups, in many cases functional groups make it much easier to examine and compare the seasonal and interannual changes in various lake types and to evaluate the responses to environmental conditions and changes (Weithoff et al. 2001, Kruk et al. 2002, Naselli-Flores et al. 2003). The functional groups relevant to this work are described in Table 4.

1.6.3 Steady state & intermediate disturbance hypothesis

The classical scenario of seasonal changes is directional with different functional groups following each other: growth of ruderal (R) species is followed by fast growing colonist (C) species, which are then replaced by stress tolerant (S) species. If the environmental conditions remain constant for a long period, e.g. during thermal stratification, large numbers

Table 3. Main characteristics of primary strategies (C S R) of phytoplankton based on Reynolds (1988).

	C: colonists	S: stress tolerants	R: ruderals
morphology	small, high SA/V-ratio	large, low SA/V	intermediate to large, high SA/V
strengths	efficient nutrient uptake, wide temperature tolerance	resistant to sinking and grazing high nutrient-storage capacity, tolerance of low nutrient concentrations	tolerance of low temperature and light, high metabolic activity
weaknesses	sensitive to light, susceptible to grazing	sensitive to temperature, low growth rate	high sinking rate
Optimal season	early summer	late summer	spring & autumn
Examples	*Chlamydomonas*	*Uroglena*	*Asterionella*

SA/V = surface area to volume

Table 4. Basic characteristics of selected functional groups of phytoplankton according to Reynolds (2006).

	Habitat	Typical representative	Tolerances	Sensitivities
A	Clear, often well-mixed, base poor lakes	*Cyclotella comensis*	Nutrient deficiency	pH rise
B	Vertically mixed, mesotrophic small-medium lakes	*Aulacoseira subarctica*	Light deficiency	pH rise, Si depletion, stratification
C	Mixed, eutrophic small-medium lakes	*Asterionella formosa*	Light, C deficiency	Si exhaustion, stratification
N	Mesotrophic epilimnia	*Tabellaria, Cosmarium, Staurodesmus*	Nutrient deficiency	Stratification, pH rise
P	Eutrophic epilimnia	*Fragilaria crotonensis*	Mild light and C deficiency	Stratification, Si depletion
T	Deep, well-mixed epilimnia	*Mougeotia*	Light deficiency	Nutrient deficiency
X3	Shallow, clear, mixed layers	*Chrysococcus*	Low base status	Mixing, grazing
X2	Shallow, clear mixed layers in meso-eutrophic lakes	*Chrysochromulina*	Stratification	Mixing, filter-feeding
E	Usually small, oligotrophic, base-poor lakes or heterotrophic ponds	*Dinobryon, Mallomonas*	Low nutrients	CO_2 deficiency
F	Clear epilimnia	colonial chlorophytes	Low nutrients	? CO_2 deficiency, high turbidity
U	Summer epilimnia	*Uroglena*	Low nutrients	CO_2 deficiency
L_o	Summer epilimnia in mesotrophic lakes	*Peridinium willei*	Segregated nutrients	Prolonged or deep mixing
L_m	Summer epilimnia in eutrophic lakes	*Ceratium, Microcystis*	Very low C, stratification	Mixing, poor light
Q	Small humic lakes	*Gonyostomum*	High colour	?

of species may disappear due to competitive exclusion (Hardin 1960). These conditions are favourable for the late successional species (S-strategists), and steady state condition will be achieved. The steady state, successional climax, equilibrium state, or pronounced dominance pattern, just to name a few of the terms used in this context, is defined as a period where a maximum of three species comprise 80% of total biomass for at least three weeks without considerable variation in total biomass (Sommer et al. 1993). Besides competition, also many species-specific abilities, such as mixotrophy or shade adaptation can lead to steady state (Morabito et al. 2003, O'Farrell et al. 2003, Rojo & Álvarez-Cobelas 2003). Steady state assemblages are most often consisted of cyanoprokaryotes or non-edible large-sized phytoplankton (functional groups L_o, C, P, T, F, L_m, Q, see Table 4) (Naselli-Flores et al. 2003). According to Salmaso (2003), the equilibrium or steady state conditions are most likely to develop in large and deep lakes with low water renewal times and moderate trophic states. In oligotrophic lakes the steady state conditions are said to be unlikely (Dokulil & Teubner 2003), unless there is some additional stress factor involved, such as harsh climate, extreme acidity or high salinity (Padisák et al. 2003, Willén 2003).

The intermediate disturbance hypothesis (IDH), originally proposed by Connell (1978) in order to explain the diversity in tropical rain forests and coral reefs, states that species diversity is affected by disturbances. Based on the hypothesis, the diversity is low right after the disturbance (only R-strategists) and when the system has had enough time to proceed to the equilibrium stage (only S-strategists). The diversity is high when disturbances occur either at an intermediate frequency or with intermediate intensity (Connell 1978). In lakes, a change in thermal structure can be considered as a disturbance, since it changes the competitive conditions by altering e.g. nutrient and light availability (Reynolds 1993). Experimental work (Sommer 1995) and simulated modelling (Elliott et al. 2001a & b) have confirmed the applicability of IDH in phytoplankton communities, with highest levels of diversity found when the frequency of disturbance is two to four algal generation times (Reynolds 2006). In such conditions co-occurrence of species with various strategies is possible. In this thesis all the listed conceptual themes are discussed in terms of subarctic lakes.

1.7 Objectives of the study

The main objectives of this work were

1. To study the **species distributions and biodiversity** of phytoplankton in European mountain lakes and more closely in subarctic and arctic lakes in Finnish Lapland.
2. To identify the key **environmental factors** that are affecting algal distributions in various regions, and to assess the possible use of **phytoplankton in classification** of arctic/alpine lakes and as a descriptor of their ecological status.
3. To identify the **taxonomical and functional groups** of species which are characteristic to certain lake types; being the most dominant algal group in the area, chrysophytes were chosen for a more detailed study.
4. To study the **seasonality and interannual variation** of phyto-plankton species, especially in relation to climatic factors, in order to get

more information about the possible impacts of environmental change on phytoplankton dynamics in subarctic lakes.

5. To study the limnology during **springtime**, the most dynamic season in subarctic lakes, and to assess the magnitude and effects of acid pulses related to meltwaters.

2 Summary of the papers

Paper I compares the phytoplankton assemblages of high-mountain and high-latitude lakes in various parts of Europe. The lakes were mostly dominated by flagellates (chrysophytes, cryptophytes and dinoflagellates). Although subarctic and alpine lakes have several comparable environmental features, they are characterised by their own typical algal compositions, mostly driven by differences in geographical and catchment-related features. In general, Conjugatophyceae are characteristic to high-latitude Finnish lakes and Dinophyceae to Eastern Alps, whereas Chrysophyceae exist as different functional groups in different areas.

Paper II aims to identify the typical algal assemblages of different types of lakes in Finnish Lapland, and their relationship to environmental factors. Most lakes were dominated by chrysophytes or dinoflagellates, or functional groups E, L_o, U and F. Based on the phytoplankton species distribution, five distinct lake groups were identified. Most important environmental factors determining the algal distribution were related to water chemistry, whereas geographical factors seemed to be unimportant.

Paper III is a study on the biogeography of chrysophyte species in Finnish Lapland. Chrysophytes are often noted to be the dominant algal group in arctic and subarctic lakes, and they dominated in 45% of the lakes in this study. The most important environmental factors explaining the distribution of chrysophyte species were SiO_2, pH and altitude. The identified species showed different preferences with respect to environmental variables, some species being widely distributed, while others had a very narrow range of occurrence.

Paper IV focuses on the seasonal succession of phytoplankton in the oligotrophic, dimictic Lake Saanajärvi. The aim of the study was to identify the factors that regulate the seasonal and interannual variability in phytoplankton biomass and species structure. Phytoplankton community in Lake Saanajärvi is mostly dominated by chrysophytes and occasionally by diatoms. Based on CCA, water temperature, Ca and TN proved out to be significant in explaining the phytoplankton dynamics. Interannual differences in algal biomass seemed to be linked to the length of the ice-free season, whereas the level of thermal stability has an effect on algal biodiversity.

Paper V is a study of limnological changes and the effects of run-off in a subarctic lake during the spring melt period. The intensity of spring processes (dilution, pH decline etc.) seems to vary considerably from year to year, depending mainly on winter precipitation. No distinct pH decline was seen during the study year, and in general the effects of acid meltwaters seem to be restricted to the surface layers of the water column. In contrast to many arctic and subarctic lakes, no phytoplankton spring maximum was detected.

3 Materials and methods

3.1 Study area

Paper **I** covers a large geographical area, including a large set of high-mountain and high-latitude lakes located in the Alps, the Rila Mountains and in the Finnish Lapland. All the lakes are located above the local timberline. Vegetation cover is scarce and mostly composed of alpine meadows, sparse shrubs, mosses, grasses and sedges. Lakes in the Finnish Lapland are considerably larger (but not deeper) and have longer ice cover period than the lakes in the Alps and the Rila Mountains. The majority of the lakes have no intensive direct human impact, but some are affected by acidification processes, pasture, tourism activities and fish introduction.

Papers **II** and **III** include 33 lakes from the Northwest and Northeast Finnish Lapland (Figure 6). All lakes are located above the treeline (167–1024 m.a.s.l.), about 200–450 km north of the Arctic Circle, in the transition zone between the North Atlantic oceanic climate and the Eurasian continental climate. Catchment areas are barren and free from direct human activity. Most of the lakes are small and shallow waterbodies that do not stratify during summer (cf. Figure 3).

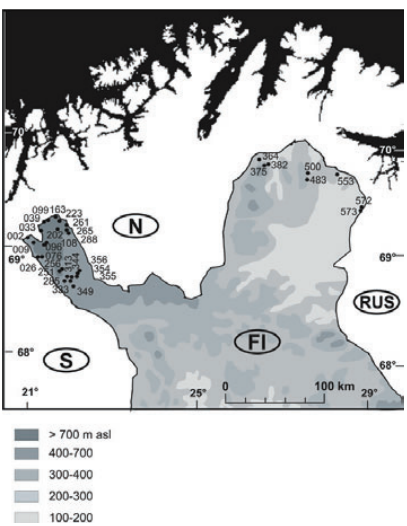

Figure 6. Map of the study area and the location of the study lakes in papers II & III.

Lake Saanajärvi

Papers **IV** and **V** focus on Lake Saanajärvi, a small (70 ha) oligotrophic clear-water lake located in Northwest Finnish Lapland above the treeline (Figure 7). The mean annual temperature in the area is -2.3 °C and the growing season is ca. 101 days long (Drebs et al. 2002). In the area, most of the annual precipitation comes as snow, and 80% of precipitation runs to waterbodies. The catchment area, 460 ha, is covered by subalpine vegetation and bare rocky surfaces. Lake Saanajärvi is free from ice for about 3–4 months (July–October). The lake is dimictic having a short spring overturn, summer stratification period and a relatively long autumn overturn.

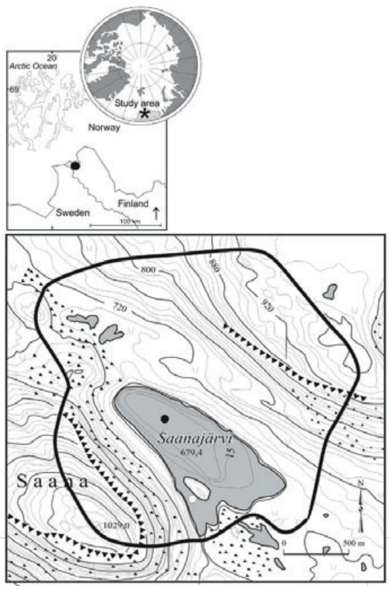

Figure 7. Map of Lake Saanajärvi. Black solid line = boundary of the catchment area.

3.2 Sampling

For papers **I**, **II** and **III** sampling was carried out during thermally mixed conditions in late summer–early autumn to assume similar conditions between sites. All lakes were sampled once, mostly from 1 meter's depth, covering all the basic physical, chemical and biological parameters (cf. Table 5). In addition, catchment and location variables (such as lake dimensions, catchment boundaries, topographic indices, catchment landcover and geology, lake surface elevations, and relative altitudes) were delineated from digital topographic and bedrock geology maps and a digital elevation model.

Paper **IV** covers two open water seasons, in which sampling for water chemistry and chl-a was carried out once a week (1996) or every other week (1997) for most of the sampling period. Phytoplankton samples were collected every other week during both open water seasons. Samples for water chemistry were taken from ten different depths, whereas phytoplankton was sampled from five depths.

For paper **V,** Lake Saanajärvi was intensively sampled during the spring of 1999. Samples for water chemistry were taken once a week from the deepest point of the lake (10 different depths), from the northwest shoreline (3 depths) and from the inlet. Samples for phyto- and zooplankton were taken every other week from the deepest point of the lake from five depths. In addition, snow samples were taken three times and analysed for their basic chemistry.

3.3 Physical, chemical and biological determinations

The methods used in the studies I-V are summarized in Table 5.

Phytoplankton taxonomy and nomenclature is primarily based on Bourrelly (1966, 1968), Komárek & Fott (1983), Starmach (1985), Tikkanen (1986) and John et al. (2002). According to EMERGE protocols, each taxon has been identified with an 8-character code (4 for the genus and 4 for the species). In cases where the identification is restricted to the genus level the last part of the code has been replaced by a progressive number together with the lake district acronym (e.g. *Cosmarium* sp. found in Northern Finland = COSM01NF).

3.4 Statistical analyses

The statistical analyses used in the papers I-V are summarized in Table 5.

4 Results and discussion

4.1 Regional biogeography and the role of environmental factors in species distribution

The lakes included in the European-wide survey of high-altitude and high-latitude lakes (Paper I) share some common features such as small lake size, shallowness, low water mineralization, low buffering capacity and low nutrient concentrations. Phytoplankton communities in all lakes were mostly dominated by flagellated species belonging to Chrysophyceae, Cryptophyceae and Dinophyceae. Flagellates often dominate the phytoplankton of nutrient poor arctic and alpine lakes (Kalff 1967b,

Table 5. Limnological and statistical analysis used in papers I-V.

Measurement	Method	References
Oxygen	in situ measurement, O_2 probe	HANNA Instruments
pH	in situ measurement, pH electrode	HANNA Instruments
Conductivity	in situ measurement, conductivity probe	HANNA Instruments
Alkalinity	Potentiometric titration	SFS 3005
NO_2+NO_3-N*	Spectrophotometric determination	SFS 3030
NH_4-N*	Spectrophotometric determination	SFS 3032
TN*	Spectrophotometric determination	Valderrama (1981), Eaton (1995)
PO_4-P*	Spectrophotometric determination	SFS 3025
TP*	Spectrophotometric determination	Valderrama (1981), SFS 3025
Ca, Mg, Na*	Flame atomic absorption spectrometric method	Eaton (1995)
SO_4^{2-}-S	Turbidimetric method & spectrophotometric determination	SFS 5738
Cl	Colorimetric method & potentiometric titration	Grimshaw et al. (1989)
SiO_2*	Spectrophotometric determination	
DOC	High temperature combustion	Salonen (1979)
Colour	Spectrophotometric determination	SFS-EN ISO 7887
$\delta^{18}O$	Mass spectrometer	
Chl-a	Fluorometric method	Jefferey & Humphrey (1975)
Phytoplankton	Settling chamber technique	Utermöhl (1958)
Zooplankton	Settling chamber technique	Utermöhl (1958)

* = analysed in the Lapland Regional Environment Centre or Laboratory of Physical Geography

Numerical technique	Method	References
Phytoplankton diversity	Shannon index H'	Krebs (1999)
Phytoplankton evenness	Pielou's J'	Pielou (1975)
Year-to-year differences in H' and J'	paired t-test	Hollander & Wolfe (1999)
Limnological differences among lake districts	one-way ANOVA	
Relationship between phytoplankton and physico-chemical parameters	RDA	ter Braak (1996)
Relationship between phytoplankton and physico-chemical parameters	CCA	Jongman et al. (1995), ter Braak & Smilauer (1998)
Distribution of environmental variables among the lakes in different lake districts	PCA	ter Braak & Smilauer (1998)
Amount of variance accounted for by different variable groups	analysis of variance partition	ter Braak & Smilauer (1998)
Lake classification based on phytoplankton communities	Complete linkage cluster analysis	

Moore 1979, Rott 1988, Nauwerck 1994, Tolotti 2001, Tolotti et al. 2003). Due to their generally small cell size, motility and the ability of mixotrophy by several species (Holen & Boraas 1995), flagellates are well adapted to the prevailing conditions in these lakes. The large proportion of chrysophytes in the study lakes (dominating in 45% of the study lakes in Finnish Lapland and in several high-altitude lakes) is not surprising, since they are known to have low nutrient requirements and low temperature optima (Reynolds 1984b). The characteristic phytoplankton species of Northern Finland include many species from various taxonomic groups indicative of or tolerant to oligotrophic conditions, such as the chrysophytes *Dinobryon cylindricum*, *Uroglena* sp., the diatoms *Aulacoseira alpigena*, *Cyclotella comensis,* the chlorophytes *Coenocystis subarctica, Sphaerocystis* sp., and the desmids *Staurodesmus* spp. and *Cosmarium* spp. (Reynolds 2006). Many of the lakes in Finnish

Lapland were heavily dominated by only a few phytoplankton species, and this pronounced dominance pattern was most common in lakes located in high altitudes or lakes with some additional stress factor, such as low conductivity or low pH.

Based on the study of chrysophyte distribution in Finnish Lapland (Paper III) and other works covering larger areas (Eloranta 1995, Siver 1995), it seems that many chrysophyte species with a relatively narrow range of tolerance could be useful as biological indicators. However, for many of the small-sized chrysophyte species, proper identification is problematic and requires methods (scanning electron microscopy (SEM) and transmission electron microscopy (TEM)) not commonly available or used in routine phytoplankton analyses.

When considering the high-altitude and high-latitude lakes on a large (European-wide) scale (Paper I), the range of geographical and catchment-related features such as altitude, ice cover duration and bedrock-type becomes large, and these differences are reflected by different phytoplankton species composition and functionality between different areas. In this study, the high-latitude lakes of Finnish Lapland were separated from high-altitude mountain lakes in many respects, also regarding the phytoplankton composition. Especially characteristic to the shallow lakes of Finnish Lapland seem to be the high species richness and abundance of desmids, also noted by Eloranta (1986) and Kristiansen (1964). Desmids seem to be especially characteristic of oligotrophic lakes with low alkalinity and neutral to acid pH (Happey-Wood 1988), which might explain why they are well represented in the lakes of Finnish Lapland, but not in the more alkaline high-altitude lakes of the same study (Paper I). High pH has been shown to have an inhibitory effect on photosynthesis and growth of at least some desmid species (Spijkerman et al. 2004). There have been suggestions that oligotrophic desmid species might be restricted to free CO_2 as their carbon source for photosynthesis (Moss 1973), but laboratory experiments have showed several carbon uptake mechanisms among desmids (Spijkerman et al. 2005).

When considering the lakes located in smaller regions, water chemistry seems to play a predominant role in determining algal species composition (Moore 1979, Duthie & Hart 1987, Larson et al. 1998, Tolotti 2001) and the spatial distribution of species assemblages is often irregular (Eloranta 1986, Tolotti et al. 2003). This was also the case in Finnish Lapland (Papers II & III, Figures 8 & 9), although the lakes were widely distributed, and represented different environmental, altitudinal and geomorphological settings. The most important single factors determining the species distribution in Finnish Lapland were conductivity, SiO_2, pH and altitude (Papers II & III). Altitude and the associated changes in environmental conditions have proven to be very important in influencing the species richness, distribution and biomass in arctic and alpine lakes (Moore 1979, Larson et al. 1998, Tolotti 2001, Tolotti et al. 2003). According to Nauwerck (1994), the relative importance of chrysophytes increases with increasing altitude. In the somewhat narrower altitude range of the NF (=Northern Finland) EMERGE study where all the lakes were located above the treeline, no such relationship was detected. The role of nutrients, especially phosphorus and nitrogen, could not be fully detected in this study, most likely due to the narrow range of nutrient concentrations among the study lakes, and the fact that inorganic nutrients were below

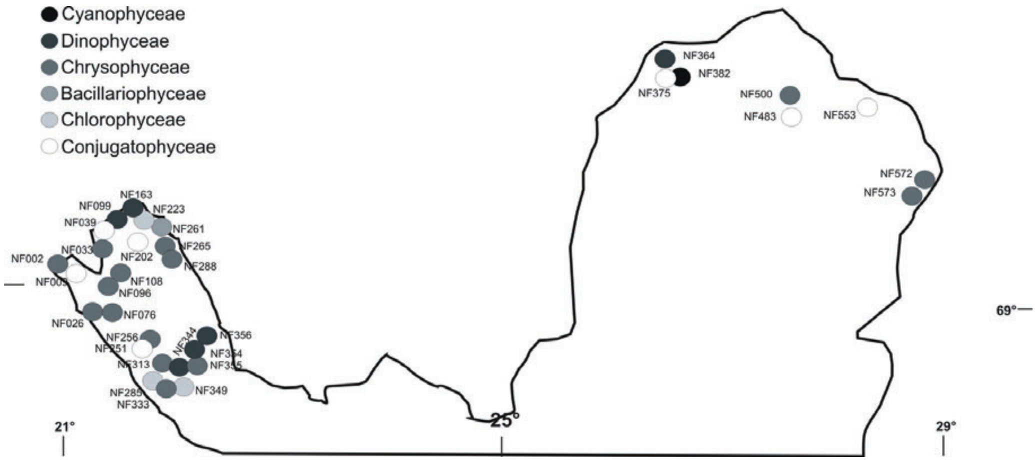

Figure 8. Dominant phytoplankton groups in terms of biomass in different study lakes.

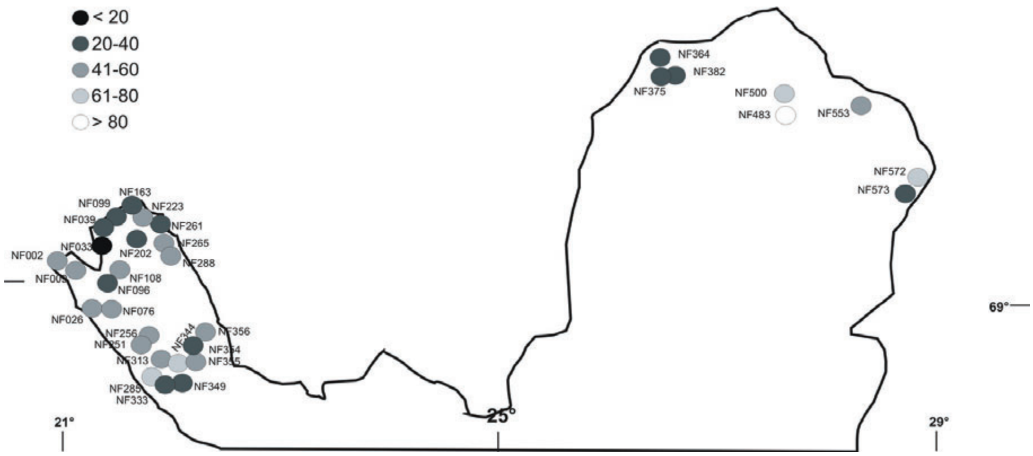

Figure 9. Species richness in different study lakes.

detection limit in many cases. The importance of nutrients in determining species composition and total biomass has been noted in many comparable studies (Moore 1979, Holmgren 1983, Larson et al. 1998, Tolotti 2001, Tolotti et al. 2003). There is an ongoing discussion whether the arctic lakes are typically limited by nitrogen or phosphorus or both (Gregory-Eaves et al. 2000, Levine & Whalen 2001, Bergström et al. 2005). Based on the analysis by Flanagan et al. (2003), the lower primary production of arctic lakes compared to temperate lakes is not simply accounted for by the lower nutrient levels, but also other abiotic and biotic factors, such as low temperature and a short growing season, suppress the production levels.

4.2 Classification of arctic lakes by phytoplankton composition and functional groups

Subarctic lakes in northern Scandinavia have previously been classified based on their phytoplankton communities by Holmgren (1983) and Eloranta (1986). In a survey of lakes in NE Finnish Lapland, Eloranta (1986) identified six lake groups (Chrysophyceae type, Mixed type, Bacillariophyceae type, Cyanophyceae type, Chlorophyceae type and Dinophyceae type), which differed from each other mainly in conductivity, COD (chemical oxygen demand) and phytoplankton biomass. The water chemistry of the lakes in Eloranta's study is similar to that of the lakes in our study (Paper II), with the exception of nutrient concentrations which were generally lower in the EMERGE data set. Characteristic algal species of various lake types are not given by Eloranta (1986), but on the whole, there is good concordance in the dominant species between the two studies. In both studies the lakes dominated by diatoms had highest conductivity, whereas lakes dominated by cyanophytes had highest nutrient concentrations and high pH, and lakes dominated or subdominated by chlorophytes had low conductivity. Based on his own work and other phytoplankton studies conducted in arctic and subarctic areas, Holmgren (1983) has identified four different lake types (Table 6), of which especially the Chrysophyceae-diatom lakes and EMERGE lake group 1 (paper III) share many similarities (e.g. large size and depth, clear water, relatively high conductivity). Also Holmgren's Chrysophyceae-Dinophyceae lakes have similar features to EMERGE lakes, especially to groups 2A and 2D. In contrast to Holmgren (1983), cryptophytes were not very common in this study or in Eloranta's (1986) lake set.

Functional groups are especially useful in lake classification, since they describe the groups of species that frequently coexist and increase or decrease simultaneously. Thus, species in the same functional group do not necessarily come from the same taxonomical group, but they share similar ecological requirements. For example, chrysophytes are common in both Finnish Lapland and Alps, but many of the characteristic species are different and belong to different functional groups (Paper I). In Northern Finland the functional groups X3

Table 6. Lake-groups and their characteristic functional groups identified in the subarctic, arctic and alpine areas.

Lake type	Spring	Summer	Autumn
Reynolds (2006), according to Holmgren (1983)			
1. Chrysophyceae lakes	X3	E, Y	E
2. Chrysophyceae-diatom lakes	X2, X3, E, Y	A, (B?)	A, Y, L_o
3. Chrysophyceae-Cryptophyceae lakes	X2, X3, E	B, Y	B, Y
4. Chrysophyceae-Dinophyceae lakes	Y	U, B, F, L_o	L_o
Emerge NF lakes (paper III)			
1. Diatom-Chlorophyceae lakes (1)			C, N
2. Chrysophyceae-Dinophyceae (2A)			E, L_o, X3
3. Chrysophyceae-Chlorophyceae (2B)			U, N, L_o, X3
4. Cyanophyceae (2C)			S1, K
5. Chrysophyceae-Dinophyceae (2D)			L_o, E, F
Lake Saanajärvi (paper IV)			
1996	U, X3	U, L_o -> A	A, U -> A, X3
1997	X3, X2	U	U, X3 -> U, F
Emerge high mountain and high latitude lakes (paper I)			
1. Group A (Northern Finland)			E, U, L_o, X3, X2
2. Group B (SW Italian Alps)			X2, E, A
3. Group C (Eastern Alps)			X2, X3, L_o, U
4. Group D (Rila Mountains)			Y

and E are more common during the autumnal mixing period, while X2 is more common in the Alps. The group X2 is more associated to meso- and eutrophic lakes, whereas groups X3 and E are indicative of oligotrophic lakes (Reynolds 2006, Table 4). Of the characteristic functional groups observed in NF EMERGE lakes, groups E, F, U and X3 are indicative of oligotrophic lakes, whereas L_o and N are more indicative of mesotrophic lakes, but tolerate segregated nutrients (Reynolds 2006, Table 4). Table 6 presents a comparison of the lake classifications in subarctic and alpine areas using the functional groups approach. These groups and their characteristic features are listed in Table 4 and fully explained in Reynolds (2006). Table 6 shows that although the same taxonomical groups might characterise the lake groups in different locations, the dominant species can be different and belong to different functional groups. This is especially seen with diatoms (characteristic species belonging to either functional groups A, B or C) and chrysophytes (characteristic species belonging to functional groups E, U, X3 and X2). In that way, functional groups give complementary information about the phytoplankton communities and their living conditions.

4.3 Seasonality of phytoplankton: the importance of spring events and other controlling factors

Seasonal distribution of phytoplankton in subarctic lakes varies from unimodal to bimodal, but due to the short openwater period it seems that most lakes only have one annual biomass maximum (Nauwerck 1968, Pechlaner 1971, Winberg et al. 1973, Kalff et al. 1975, Holmgren 1983, Miller et al. 1986, Shortreed & Stockner 1986). A spring peak of phytoplankton, sometimes occurring already under ice, is a common feature in both arctic and alpine lakes, and is related to increased light intensity, long periods of daylight and excess nutrients after winter mineralization (Kalff et al. 1975, Holmgren 1983, Pugnetti & Bettinetti 1999). In Lake Saanajärvi the conditions are unfavourable for the formation of such a peak, mainly because the somewhat nutrient-rich melt waters do not mix efficiently into the lake water, but exit the lake trough a surface outflow within a few days. Therefore, organisms can hardly profit from this extra nutrient source, but instead they are suffering from increased flushing and drastic changes in light conditions. In general, when flushing slows down, the algae are still stressed by high dilution, decreased pH and fluctuations between exposure to harmful radiation levels and light limitation (e.g. Catalan 1992). In addition, there is a relatively high grazing pressure during spring in Lake Saanajärvi, since the dominant zooplankton species, the copepod *Eudiaptomus graciloides,* has its peak abundance during early spring. As a consequence, phytoplankton biomass is usually very low during springtime in Lake Saanajärvi (Papers IV & V). Phytoplankton biomass then increases gradually towards the autumn so that the maximum biomass is reached during the end of the summer stratification or at the beginning of the autumnal overturn.

During the two-year study of phytoplankton in Lake Saanajärvi (Paper IV), small C-strategist chrysophytes, mainly *Pseudopedinella* sp., *Chrysococcus* spp and small unidentified flagellates dominated the spring mixing period. In 1996 the colonial chrysophyte *Uroglena* sp., some dinoflagellates and cryptophytes were also common. Most of the characteristic spring taxa belonged to the functional groups X3 and X2, both of which favour mixed layers of shallow and clear waters. During the summer stratification period, chrysophytes (mainly *Uroglena* sp.) dominated the phytoplankton assemblage. This was followed by the dominance of centric diatoms in 1996, whereas in 1997 the chrysophytes stayed dominant throughout the summer. Dinoflagellates were subdominant in both years. Expressed as functional groups, the first part of the summer of 1996 and the whole stratification period of 1997 were dominated by the S-strategist group U, which typically occurs in summer epilimnia, tolerates low nutrient levels but is sensitive to CO_2 deficiency. In 1996 the functional group U was followed by the R-strategist group A (Table 6), which typically favours clear and well-mixed base-poor lakes and tolerates low nutrient levels, but is sensitive to a pH rise (Reynolds et al. 2002). During the autumnal overturn in 1996 the dominant taxa were centric diatoms (functional group A) and *Uroglena* sp. (functional group U). Later, as water temperature continued to decrease and inverted thermal stratification started to develop, *Uroglena* sp. was replaced by *Chrysococcus* sp. belonging to X3. In the autumn of 1997 *Uroglena* sp. dominated throughout the season, first together with X3 species and later with colonial chlorophytes belonging to F.

Partial Redundancy Analysis (RDA) (paper V) and Canonical Correspondence Analysis (CCA) (paper IV; Table 5) were used to find out how the chemical and physical factors of the lake explain the seasonal distribution of phytoplankton. The most important factor explaining the species distribution during the spring was the ice phenology, whereas during the open water season the most important explanatory factors were total nitrogen, calcium and water temperature. Naturally, the ice cover does not directly affect the algal communities, but together with snow it blocks most of the solar radiation and prevents wind-induced mixing. Heavy flushing was also linked to the presence of ice cover, since most of the snow melted while the lake was still ice covered. It has been demonstrated earlier that flushing rate can have a marked effect on phytoplankton community and biomass in small boreal lakes (Similä 1988, Jones 1991). In general, nutrient concentrations were low throughout both studies, which is probably the reason why their role as explanatory factors remained low. Low nutrient levels probably favoured chrysophytes, which have superior abilities for storage and growth under low phosphorus levels (Sandgren 1988). In addition, many chrysophyte genera common in Lake Saanajärvi, such as *Uroglena* and *Dinobryon* are mixotrophic, which gives them more opportunities under nutrient limitation. The role of Ca in regulating species composition and dynamics is somewhat unclear, but at least certain desmid species seem to have narrow tolerance to calcium concentration, and most of them, together with many chrysophyte species, favour calcium-poor waters (Wetzel 2001, Reynolds 2006). Calcium has a central role in the dynamics of pH, carbon dioxide and bicarbonate, influencing the supply of photosynthetically available carbon and the buffering capacity of water (Reynolds 1984b, Wetzel 2001). Chrysophytes are especially sensitive to high Ca concentration and pH rise, since they are restricted to dissolved free CO_2 as their source of carbon (Sandgren 1988) and many species seem to lack carbon-concentrating mechanisms (CCM) (Raven et al. 2005). It is likely that Ca itself was not the main factor affecting the species composition in Lake Saanajärvi, but represented a surrogate variable reflecting other linearly related parameters such as major ions, pH, alkalinity and conductivity, known to play an important role in algal composition (Moss 1973). Water temperature is an important factor controlling the growth rates and distribution of many taxa (Reynolds 1984a, Flanagan et al. 2003), and especially chrysophytes and diatoms are most competitive at low water temperatures (Hutchinson 1967, Sandgren 1988). Duthie & Hart (1987) conclude that the main factor controlling the diversity and biomass of phytoplankton in northern lakes seems to be the temperature, whereas the distribution of individual species is influenced by water chemistry. Although the role of temperature was not seen in the biogeographical part of the present study (Papers I, II & III) (because the lakes were sampled during the mixing period), its role was clearly seen in Lake Saanajärvi: the main environmental gradient in CCA was formed by the seasonal temperature changes (Paper IV).

4.4 Interannual variation and the effects of climate related factors on algal seasonality

Although the seasonality of phytoplankton in a given lake seems to follow a regular pattern, marked interannual differences in species composition and biomass has often been noted, especially in arctic and alpine lakes (Kalff et al. 1975, Salmaso & Decet 1997, Hinder et al. 1999). The main sources of the ecosystem variability in mountain lakes results from meteorological forcing (Catalan et al. 2002). Also, interannual differences in algal species composition have been linked to differences in water column stability as well as meteorological and hydrological events (Sommer 1985, Harris 1986, Goldman et al. 1996, Salmaso & Decet 1997, Hinder et al. 1999). Compared to temperate lakes, the thermal stability of arctic lakes is generally low, due to heavy wind stressing and low water temperatures resulting in alternating mixing and stratified periods.

Timing, intensity and length of different thermal periods play an important role in phytoplankton species succession and periodicity (Reynolds 1980). In Lake Saanajärvi there were marked differences in the weather and the physical properties of the lake between the two studied open-water seasons (Paper IV: 1996 & 1997), as well as between the two studied spring periods and the preceding winters (Paper V: 1997, 1999). The open-water season of 1996 was longer, but due to heavy winds the stratification was weaker and lasted for a shorter period than in the following year. The conditions in the summer of 1996 were at first most suitable for the large colonial *Uroglena* sp., but later it was replaced by centric diatoms. In 1997 *Uroglena* sp. seemed to be most competitive taxon throughout the summer. The main differences between the two study years are summarized in Figure 10. The pronounced dominance of the S-strategist *Uroglena* sp. in 1997 (Figure 10b) with stronger stability of the water column is consistent with the results of Weithoff et al. (2001), who conclude that the relative success of S-strategists is greater with more stable stratification. Although *Uroglena* sp. favours stratified conditions (Reynolds 1984b), it was able to persist even during the period of autumnal overturn in 1997. As a consequence of the long stratified period, a state close to equilibrium or steady state was reached in the late summer of 1997, when only a few species of chrysophytes (mainly *Uroglena* sp.) contributed more than 80% of the standing biomass for a relatively long period. The results are supported by experimental work conducted by Teubner et al. (2003), where a steady state condition was associated with the increase of thermal stability.

As well as species composition, total phytoplankton biomass and diversity were also

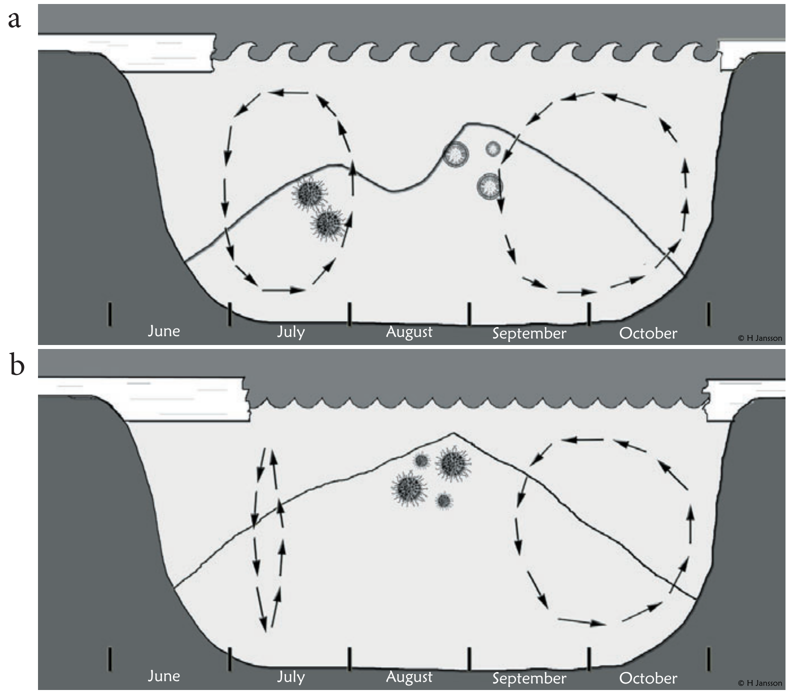

Figure 10. Schematic picture of openwater seasons a)1996 and b) 1997 in Lake Saanajärvi. Arrowcircles indicate the periods of overturn, solid line indicates the development of phytoplankton biomass. The drawings at July 1996 and August 1997 indicate dominance of Uroglena, drawings at August and September 1996 indicate dominance of Cyclotella.

affected by factors related to temperature and thermal stability. Both chl-a and maximum biomass were higher in 1996, most likely as a result of higher temperatures and a longer ice-free season (Paper IV). The more stable weather conditions and a longer stratification period lead to a lower diversity of phytoplankton in the summer of 1997, which is consistent with the findings by Harris (1986) and the basic idea of the intermediate disturbance hypothesis (Connell 1978). The summer of 1996 with more wind-induced turbulence and a shorter stratification period made the co-existence of species with different strategies possible, while in 1997 the S-strategistic *Uroglena* sp. was able to outcompete others.

In addition to the factors related to temperature and thermal structures of lakes, also other climatic factors of potential importance to phytoplankton, such as precipitation, show noticeable year-to-year changes. In the Kilpisjärvi area, the difference in precipitation was especially big between the two years discussed in Paper V: total precipitation in e.g. April 1997 was 152 mm and only 34 mm in 1999, resulting in 133 and 21 cm deep snow cover in mid-May of the same years, respectively (Figure 2). Rapid melting of the snowpack resulted in an episodic decline in surface water pH from 6.7 to 5.4 and conductivity from 31.6 to 8.5 $\mu S\ cm^{-1}$ in 1997, but no pH decline was detected in 1999 with exceptionally thin snowpack. In addition to changes in pH and conductivity, higher nitrate concentrations were detected in the surface water during the melting period in 1997. Because Lake Saanajärvi has a good buffering capacity, the possible pH decline is short-lived. Results of this work are consistent with other studies, which show that the melt waters do not usually mix effectively with the lake water, but being lighter and more dilute, form a major part of the outflow (Hobbie et al. 1983, Similä 1988). Mixing of the different water masses is further hindered because the ice cover prevents wind-induced mixing (Bergmann & Welch 1985). Consequently, plankton is probably little affected by acid pulses in Lake Saanajärvi, which is in accordance with some other studies from Finnish Lapland and Kola Peninsula that demonstrate little biological impacts due to acidification (Korhola et al. 1999, Weckström et al. 2003). However, the vulnerability of arctic and subarctic aquatic biota to acid and toxic impacts is high during spring, because many stressors (e.g. low temperature, low nutrient levels, high solar radiation) operate simultaneously and many species are in their most sensitive early life stages (Catalan et al. 2002, Rautio & Korhola 2002).

5 Conclusions

The main aim of this study was to gather more information about the ecology of the phytoplankton in subarctic lake ecosystems, both in terms of their occurrence and seasonality as well as the effects of environmental factors on various phytoplankton taxa and functional groups. At present, the interactions of climatic factors with arctic freshwater ecosystems are poorly understood and the lack of detailed studies concerning arctic and subarctic lakes, especially in terms of seasonal changes, has been noted e.g. in the Assessment Report of the Arctic Monitoring and Assessment Programme (AMAP 1998) and the Arctic Climate Impact Assessment (ACIA 2005). Arctic lake ecosystems are considered to be very sensitive to environmental change and would therefore be especially suitable as “early warning systems” (Vincent et al. 1998, Flanagan et al. 2003). However, more information is needed in order to identify and project the effects of climatic and other environmental changes on different organisms and the ecosystems as whole. The use of biological indicators in lake classifications and monitoring is especially crucial in arctic lakes, where many of the chemical parameters are for most of the time generally below the detection limit of the methods. If only chemical parameters are followed in these oligotrophic systems, many differences between the lakes and especially the early ecosystem changes might remain unnoticed.

The European-wide study of phytoplankton in high-latitude and high-altitude lakes (Paper I) revealed differences between the lakes located in different mountain districts. While all the lakes located in Finnish Lapland could be considered oligotrophic or ultra-oligotrophic based on their nutrient levels, chl-a concentrations and characteristic phytoplankton taxa and functional groups, some highly productive lakes were identified in the Alps as indicating anthropogenic eutrophication. Thus, geographical and catchment-related features appeared to be most important in explaining the algal differences between the different districts, whereas differences within a district seemed to be mainly driven by lake chemistry. Especially desmids (Conjugatophyceae), dinoflagellates (Dinophyceae) and chrysophytes (Chrysophyceae) were shown to be useful for lake classification, and the application of the phytoplankton functional groups approach proved out to give additional information about the site-specific differences.

The study shows that climatic factors have a major influence on the phytoplankton species dynamics in subarctic oligotrophic lakes. The seasonal and interannual variation in temperature, wind conditions and precipitation is further reflected in algal diversity and species distribution, with species having different ecological strategies thriving in different conditions. The results of this thesis support the previous findings that strong and long-lasting thermal stability creates low-diversity conditions resembling equilibrium state, whereas windy and more variable conditions enable more diverse systems where species with different functional strategies can co-exist. The results suggest that in addition to species composition and dynamics, also total phytoplankton biomass in itself is affected by climatic factors (especially temperature).

This study agrees with the previous observations about the importance of the spring as the most dynamic season in the limnology of arctic and subarctic lakes. Spring pH depression associated with snow melt is a natural process, but it may be amplified by acid deposition during the winter months. In the Kilpisjärvi region the accumulation of anthropogenic acids is low, and dilution of the lake water caused by ion-poor melt waters is the main mechanism behind the acid pulse. There is large interannual variability in the magnitude and intensity of the acid pulse, mainly due to differences in winter precipitation. As the melt waters do not mix effectively with the lake water, the effects of the acid pulse are short-lived and mainly restricted to the lake surface.

This study showed that very diverse phytoplankton communities can be found in high-altitude and high-latitude lakes, and that phytoplankton species composition can be used in lake classifications. Phytoplankton can be useful also in studies concerning environmental change, since the species composition responds quickly to changes in thermal conditions. In the future, carefully designed experimental studies and longer time-series are needed to add to the knowledge gathered mostly by short-term lake surveys.

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